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Do Marine Turtles Use Odors to Locate Foraging Hotspots in the Open Ocean?

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ABSTRACT. – Marine turtles in the open ocean often forage in areas of enhanced productivity, but how they locate those sites and what they do once there is poorly understood. One possibility is that odors from prey might be informative. We explored those possibilities in laboratory experiments using juvenile marine turtles. We analyzed responses to an airborne by-product of predation (dimethyl sulfide or DMS) and to airborne and waterborne odors made from extracts of fresh prey (squid, jellyfish, penaeid shrimp, and algae [*Sargassum* spp.]). Observations were made in a seawater-filled arena containing an enclosed air space. Airborne odors were delivered across the water surface and waterborne odors were introduced as extracts into the water. Tethered loggerheads (*Caretta caretta*) and leatherbacks (*Dermochelys coriacea*) failed to swim “upwind” in the presence of any airborne odor, suggesting that these stimuli, alone, do not evoke orientation from a distance. Free-swimming loggerheads and green turtles (*Chelonia mydas*), presented with either an airborne or waterborne squid odor, directed bites at the tank walls, at one another, and (most frequently) at a stationary visual stimulus (a small plastic sphere) anchored under water. DMS did not evoke a comparable response. We conclude that close to productive hot spots, both air- and waterborne prey odors elicit a similar visual search for underwater prey targets. A review of the literature suggests that at a distance, juvenile turtles might use magnetic maps to locate areas that include sites of greater oceanic productivity.

KEY WORDS. – Reptilia; Testudines; olfaction; orientation; DMS; foraging; sea turtle; ontogeny

Many marine predators, among them seabirds, sharks, teleost fishes, and sea turtles, have the capacity to migrate to distant resources such as sites that are favored for foraging, breeding, nesting, and completing early development (Luschi 2013; Dingle 2014; Mansfield et al. 2014). In the case of sexually mature female sea turtles, these migratory movements are well documented, largely because the turtles come ashore to nest, which enables workers to attach tracking devices to their carapace and (once nesting is completed) chart their return movements toward foraging grounds. Return movements fall into two general categories: those shown by species that most-often return to discrete, shallow-water coastal foraging habitats (for example, loggerheads [*Caretta caretta*], green turtles [*Chelonia mydas*], and hawksbills [*Eretmochelys imbricata*]) and those shown by species that usually forage widely over vast areas of the ocean (leatherbacks [*Dermochelys coriacea*] and eastern Pacific olive ridley [*Lepidochelys olivacea*] turtles; Jones and Seminoff [2013]). For oceanic foragers, the search for prey is complicated by the vast distances involved as well as the ephemeral nature of productive oceanic areas, both in space and through time (Hays et al. 2006). Nevertheless, the turtles usually find these sites which are often associated with current convergences, upwelling zones, and underwater structures such as seamounts (Uchida et al. 1986; Andreae et al. 1994; Nevitt 2000; Polovina et al. 2006).

Turtles are thought to locate distant resources, such as nesting beaches or productive oceanic “hotspots”, by a 2-step process (Lohmann et al. 1999, 2008). During the first step, one set of cues is used to locate the general area. During the second step, other cues are used to pinpoint a more-spatially restricted goal or location. Experiments suggest that in marine turtles, the first step is preferentially based upon magnetic cues (Lohmann et al. 2004; Luschi et al. 2007). However, the turtles do not depend exclusively upon magnetic information, as displaced turtles bearing magnets still manage to return to the capture site, presumably by using alternative guideposts (Luschi et al. 2007). Alternative guideposts may be visual (Avens and Lohmann 2003; Mott and Salmon 2011), mechanical (surface waves; Salmon and Lohmann 1989; Lohmann et al. 1995), or remain unidentified.

Even less is known about how the turtles locate specific targets during the second stage, when they are relatively close to particular goals. Experiments with green turtles that nest on Ascension Island suggest odors might be involved. Ten of 18 females that were displaced 60–450 km from Ascension Island nesting beaches returned to the island. All 10 did so from a location downwind of the island (Luschi et al. 2001). A similar correlation was obtained by Hays et al. (2003). They displaced 6 females about 50 km from the island. Three of the turtles were displaced upwind and 3 were displaced downwind. One of

the turtles displaced upwind failed to return while 2 others took 10 and 27 d, respectively, to return (after swimming past the island, then turning toward it from the downwind side); all of the turtles displaced downwind returned to the island in 4 d or less (Hays et al. 2003). Unfortunately, the design of these experiments could not exclude the possibility that cues other than, or in addition to, airborne odors might also have been used (Lohmann et al. 2008).

Past research on odor reception by marine turtles has centered upon their ability to detect and exploit waterborne odors. Constantino and Salmon (2003) found that when leatherback turtles tethered inside a small pool were exposed to prey odors (of jellyfishes and ctenophores), they swam more vigorously and oriented into a water current bearing that odor. However, when a model jellyfish was presented at another location inside the pool, the turtles ignored the odor-bearing current and swam toward the model. In both instances, then, the odor acted as a releaser that triggered a hierarchically oriented response to a “directing” stimulus, with visual cues dominant over currents.

In a laboratory pool or in shallow coastal waters where the bottom is visible, turtles can determine current direction by reference to stationary objects in their surroundings, and then orient “upstream”. In the open ocean, however, detecting current flow is difficult because all objects in the environment are transported in the same direction and at the same velocity (Bradbury and Vehrencamp 2011). For that reason, sea turtles searching for productive areas in such a location might benefit by responding instead to airborne odors.

There are two advantages to responding to airborne odors. First, the turtles might be able to determine wind direction and locate the source by an anemotaxis. Such a capacity has been demonstrated for procellariiform seabirds (Nevitt et al. 1995). Second, airborne olfactory cues greatly enlarge the atmospheric fingerprint of a productive region by expanding its “olfactory landscape”. Doing so should, at least in theory, increase the probability that predators searching for those targets will succeed in finding them (Nevitt 2000).

Endres and colleagues (2009, 2012) showed experimentally that under laboratory conditions, juvenile loggerheads detect airborne odors of their commercial diet as well as dimethyl sulfide (DMS), a by-product of injured prey from productive sites where predators are actively feeding (Andreae and Raemdonck 1983; Andreae et al. 1994). Detection was measured by an increase in activity, especially circling, and by how long the turtles kept their head above the water surface, perhaps sampling the odor. Both of these parameters increased significantly when the turtles were exposed to either food or DMS odors as compared to control odors (distilled water, nonmarine aromatic compounds). While those differences unambiguously demonstrated that the turtles detected food and DMS odors, those responses provided limited insight into how the turtles might respond to natural prey odors and

then use such a response to locate productive oceanic areas. We initiated this study in part to answer that question.

We had two objectives. The first was to determine whether airborne odors (those from DMS, those from prey) might release an upwind search for a hotspot at a distance. Our second objective was to determine whether the behavioral response to prey odor detected under water differed from the behavioral response to the same odor detected in air. We hypothesized that prey odors detected under water in an open ocean environment might release a general search in the area. Taken together, these two responses to odors might enable turtles to locate distant resources (such as feeding sites in the open ocean) in the two-step process described by Lohmann et al. (1999, 2008).

METHODS

Turtle Maintenance. — Leatherback, loggerhead, and green turtle hatchlings were captured as they emerged from nests deposited on beaches in Palm Beach, Broward, and Lee counties, Florida, USA. Turtles were transported in small coolers to the Florida Atlantic University Marine Laboratory at the Gumbo Limbo Environmental Complex where basic measurements were made (of straight-line carapace length and width using calipers [accurate to the nearest 0.1 mm] and of mass [to the nearest 0.1 g] using an electronic scale). All turtles were held for 5–7 d in quarantine to ensure that they were healthy. Thereafter, each turtle’s growth and health was recorded on a weekly basis. Daily observations were made to confirm that all subjects were swimming and feeding normally. All of the turtles were exposed to a 12L:12D light cycle using UVA/UVB lights hung 0.5 m above the water surface. After experiments were completed, the turtles were taken several kilometers offshore and released in the Gulf Stream.

Loggerheads and green turtles were maintained at 25°–29°C in shallow, elongated fiberglass or polypropylene tanks with a continuous flow of filtered seawater. Up to 30 turtles were housed in each tank, with each held individually in floating perforated plastic baskets (19.5 × 12.7 × 12.7 cm). Tanks were cleaned and disinfected weekly. Turtles were fed an in-house manufactured diet consisting of ground fish (farmed tilapia or salmon), Mazuri™ freshwater turtle pellets, calcium supplement for reptiles, and unflavored gelatin.

Leatherbacks were held in tanks of similar size that contained no more than 2 turtles, each confined to a portion of the tank by a 25-cm length (tether) of monofilament line centered in the tank and positioned on a wood dowel across the top of the tank. Tethering is necessary because leatherbacks do not recognize barriers (such as the tank walls and bottom). Tethered turtles could swim in any direction and make shallow dives, but did not contact the walls or bottom of their tank. Leatherbacks swam in local seawater that was filtered through 1-µm sock

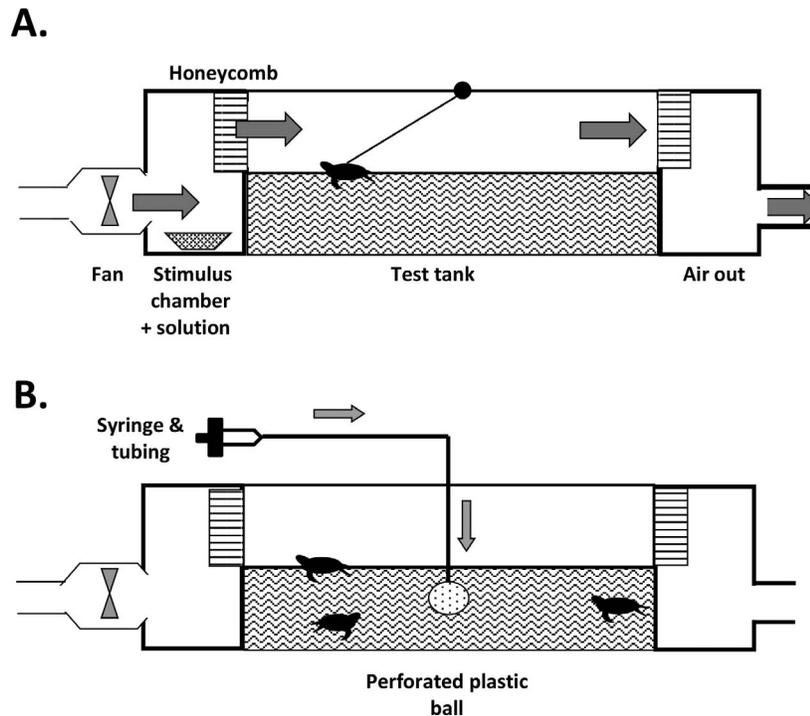


Figure 1. (A) Tank set-up for testing single turtles, swimming on a tether in the central area of the tank, for their response to airborne odors. A fan blew air over the stimulus solution and drove odor-bearing air through the stimulus chamber (left) and into the space over the water surface. The odor exited the tank through a second stimulus chamber (right). Arrows show the direction of airflow through the honeycomb. (B) Tank configuration used for experiments with groups of free-swimming turtles. Waterborne odors were introduced via plastic tubing attached to a syringe at one end, and embedded within a hollow, perforated plastic ball suspended in the water at the opposite end. Arrows show the direction of waterborne odor flow. Airborne odors were introduced as described in A, above, but with the plastic ball remaining inside the tank.

filters, purified by a protein skimmer, exposed to UV radiation to kill bacteria, and chilled to 23°–25°C (hereafter, “treated seawater”). Two-thirds of their water was changed twice daily. Complete water changes were done once weekly when tanks were cleaned and disinfected. Leatherbacks were fed a formulated diet consisting of French bread, infant cereal with iron, simethicone, baby food, ground fish or shrimp, Repti-Vite™ reptile vitamins, and unflavored gelatin.

Experimental Tank Design.—Responses of the turtles to odor stimuli were observed after each turtle was transferred to a tank designed for the presentation of either air (Fig. 1A) or waterborne (Fig. 1B) odors. Turtles were placed temporarily in a seawater-filled, square, central arena (91.5 × 91.5 × 20 cm deep) colored dark blue. During testing, the tank was covered with a clear Plexiglas™ cover that enclosed an air space (167 cm³) above the water surface. Two (opposite) sides of the cover were solid walls of white Plexiglas while the left and right sides each had a large rectangular opening (87 × 15.5 cm).

A white Plexiglas stimulus delivery chamber was located on each side of the tank. Odor solutions were placed in 1 chamber. A 20-cm-diameter fan (Model EF-8; Tjernlund Products, Inc) blew air into the chamber, over the odor solution, through a matrix of squares (1.5 cm²), and across the airspace to the opposite side of the tank (Fig. 1A). The odor exited through a 9.2-cm-diameter duct that carried air to the outside of the building. Nontoxic

white fog, produced by a fog machine (Anscam, Inc), was used to separately measure the how fast the air stream crossed the tank and to approximate the time it took to clear odorant from the airspace.

Odor solutions under water were presented through a 1.5-m-long length of 0.5-cm-diameter clear plastic tygon tubing attached at one end to a delivery syringe (Fig. 1B). The syringe was hidden from the view of any turtles swimming inside the tank. At the opposite end, the plastic tubing was inserted into a hollow, perforated, plastic ball (4-cm diameter). This tubing was used to suspend the ball at a middepth level in the center of the tank (Fig. 1B). The orientation and associated behavior of the turtles before, during, and (in some experiments) after each stimulus was presented were recorded using a video camera (Sony Handycam, model HDR-CX 160) fixed to the ceiling 2 m above the tank.

Between tests using waterborne odors the tank was drained, scrubbed with a 0.12% chlorhexidine solution, rinsed with fresh water, and then refilled with filtered treated seawater.

Odor Preparation. — DMS was presented to the turtles following a protocol similar to the one used by Endres and Lohmann (2012). We adding 1–3 drops of a 99% pure solution (Sigma-Aldrich, Milwaukee, Wisconsin, USA) to a 9-cm-diameter piece of Munktell filter paper placed on the floor of the stimulus delivery chamber. Because of its extreme volatility, the DMS odor was

prepared immediately before each presentation. Because DMS is relatively insoluble in water, no attempt was made to test its effect as an underwater stimulus.

Airborne prey odors were made from frozen samples of fresh shrimp (*Penaeus setiferus*), squid (*Illex illecebrosus*), and moon jellyfish (*Aurelia aurita*), the latter captured in the Florida Current approximately 20 km offshore. Constantino and Salmon (2003) demonstrated that extracts of moon jellyfish presented in a water current elicited a rheotaxis in leatherbacks. Homogenates were made using the protocols developed in that study. Aliquots (200 ml) of each odor were frozen, stored, and then thawed individually to room temperature immediately before use in no more than 3 trials. Prey odor solutions were presented inside a plastic container (10 × 30 × 5 cm deep), placed on the floor of the stimulus chamber, and used only for that odor. The odor of fresh *Sargassum* (collected at local beaches) was delivered by air blown across an identical plastic container filled with fresh algae. During all tests, plastic containers with prey odors were stored in an outside room until their odors were presented to the turtles. At the conclusion of each presentation, containers were removed from the test room. Odor concentrations in the air were not quantified. In pilot tests, we easily detected all of the odors as the air passed through the exhaust ducting and exited the laboratory building.

The waterborne odor was made from squid homogenate strained through 4 layers of cheesecloth to remove particles that might be detected visually. Five milliliters of this solution was diluted with 195 ml of filtered seawater and then frozen and stored in 20-ml aliquots for later use.

Responses of Tethered Turtles to Airborne DMS and Prey Odors. — Swimming leatherback (18–32 d post-emergence) and loggerhead (30–60 d post-emergence) turtles were exposed to airborne odors to determine if these stimuli would elicit upwind orientation. Each turtle was confined to the center of the tank by a 30-cm-long monofilament tether attached to the tank cover at one end (Fig. 1A). For leatherbacks, the other end of the tether was attached to a Velcro patch glued to the carapace with cyanoacrylate cement. For loggerheads, the tether was attached to a nylon–lycra harness worn by each turtle during its trial. The harness did not interfere with normal swimming and diving behavior. Each turtle was allowed to acclimate to the tank surroundings and recover from handling for 20–30 min before testing began. Once acclimated, the turtles swam slowly and returned to the surface to breathe at normal (approximately 1 min or less) intervals.

Each turtle was used in only 1 odor experiment. Leatherback DMS experiments consisted of 3, 10-min odor trials (a control trial with seawater odor, a DMS trial, followed by a second control trial identical to the first). Loggerhead trials were shorter (5 min) as these turtles were both more active and reactive. Trials consisted of a control seawater odor presentation followed immediately by a single presentation of DMS.

Prey odor trials were done with juvenile loggerheads that are omnivores and consume the same types of invertebrate prey (Witherington 2002; Jones and Seminoff 2013) that we used in our experiments. Each turtle was exposed to a 3-min control (seawater odor) followed by a 3-min prey odor (squid, shrimp, jellyfish, or *Sargassum*), presented in a random order to each turtle. None of the turtles were fed 24 hrs prior to testing to ensure that they were strongly motivated to respond to the odors. Each turtle's swimming orientation during the control and odor trial that followed was stored on video we recorded for later analysis.

Responses of Free-Swimming Turtles to Air and Water Borne Odors. — In these experiments, data collection was expedited by observing the turtles in groups composed of 3, size-matched individuals of the same species (loggerheads, 53–132 d post-emergence; green turtles, 35–90 d post-emergence). Each group swam freely inside the test tank and was used in only one test. The turtles were food-deprived for 24 h before testing and then given 30 min to acclimate to their surroundings before testing began, and responses were video-recorded for later analysis. A hollow, plastic, perforated ball was suspended at middepth in the center of the pool and used (as described above) to deliver a waterborne squid odor (Fig. 1B). At the end of the acclimation period, the turtles were tested first with a control seawater odor followed immediately by an experimental odor (either DMS or squid).

To carry out the DMS experiments, the turtles were first exposed for 5 min to a flow of air that passed over a container of filtered seawater (Fig. 1A) coupled with the injection (at the start of the trial) of 20 ml of filtered seawater into the plastic ball (Fig. 1B). Following the control period, the turtles were exposed for an additional 5 min to the airborne odor of DMS, coupled again with the injection of 20 ml of seawater into the plastic ball.

The squid odor experiment was more complex in design, as the turtles were first exposed to an airborne and then to waterborne delivery of the squid odor stimulus. The procedures used were as follows. Each experiment began with a 5-min control trial identical to the one used in the DMS tests. An experimental trial followed in which the turtle was exposed to air delivered across a container filled with squid homogenate. That exposure was coupled with the injection of another 20 ml of filtered seawater into the plastic ball. At the conclusion of that trial, the squid homogenate was removed from the room and laboratory air was fanned across the tank for 10 min to clear the tank of any residual airborne odor. Then, a second 5-min control was followed by another squid odor trial. In this trial the airborne odor was from filtered seawater and the waterborne odor was from 20 ml of squid extract injected into the plastic ball.

At the conclusion of the squid odor trials the tank was drained, scrubbed with a 0.12% chlorhexidine solution,

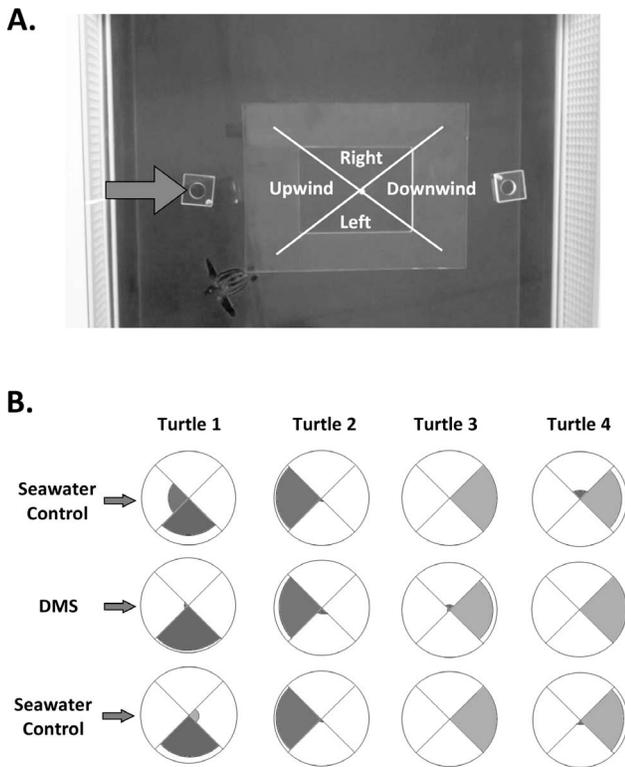


Figure 2. Above, view of the tank, looking down on a tethered leatherback. Orientation was quantified by summing the time spent in each of the 4 quarters (upwind, downwind, left, and right). Arrow shows the direction of airflow. Below, responses of 4 tethered leatherbacks during their tests, each of which lasted 30 min. The airborne odors were of seawater (2, 10-min control trials) and a 10-min DMS trial. Fill extent in each quarter of the circle diagram is proportional to the time spent in that quarter. Arrow points to the upwind quarter.

rinsed with fresh water, and then refilled with treated seawater before another group of 3 turtles was tested.

Response Analysis and Statistics. — Responses of the tethered turtles were analyzed from video recordings by summing the time (in minutes) that each turtle spent swimming in each of the 4, 90°-wide tank quarters; upwind (toward the odor flow), downwind (away from the odor flow), to the left; and to the right of the direction of airflow (Fig. 2). We also noted when and how often during their trials each turtle surfaced to breathe. We hypothesized that if the turtles found the experimental odor attractive, they might 1) change the distribution of times spent in each tank quarter, and perhaps even 2) spend more time in the upwind quarter during the experimental odor presentation than during the control presentation. We used a Wilcoxon matched pairs sign test (Zar 1999) to determine if the turtles significantly changed the time spent in any of the tank quarters during the experimental period compared with the control period. We used a chi-square (χ^2) (for leatherbacks) or a Fisher exact test (for loggerheads, when contingency tables contained cells with ≤ 5 observations; Zar 1999) to determine whether the turtles spent more time swimming in the upwind quarter of

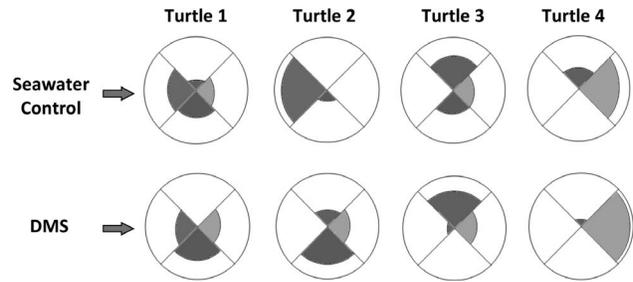


Figure 3. Responses of 4 tethered loggerheads during a 5-min control followed by a 5-min DMS trial. Format, as in Fig. 2.

the tank during the experimental presentation than during the preceding control period.

When exposed to squid odor, free-swimming turtles showed an increase in biting behavior. We used χ^2 tests (corrected for continuity; Zar 1999) to compare biting frequencies between 1) the air- vs. waterborne squid odor presentations, 2) the targets selected by each species during their exposure to the squid odor, and 3) the biting activity observed in each species.

In all statistical tests, the null hypothesis of no difference (in time spent in each quarter; in biting frequencies) was rejected when probabilities were ≤ 0.05 .

RESULTS

Odor Propagation Speed. — It took about 8 sec for an introduced cloud of fog to travel 0.9 m from one side of the tank to the other. We estimated its speed at ~ 12 cm sec^{-1} . The cloud was turbulent and showed little sign of laminar flow.

Tethered Turtles: Response to DMS Odor. — Four leatherbacks swam continuously during their trial and on average sampled the airstream by taking breaths at approximately 1-min intervals. During the initial control period, they chose an orientation direction that showed little change when exposed to DMS during the experimental period that followed (Fig. 2; 2-tailed Wilcoxon signed-rank test, $t = 8$, $n = 10$, $p = 0.84$). There were no significant differences between the observed time spent in the upwind tank quarter during the seawater control (for all 4 turtles, 13.55 min) vs. the DMS odor (10.28 min) presentations, as compared with an expected average (11.92 min; $\chi^2_1 = 0.04$, $p = 0.84$).

Four loggerheads swam continuously during their trial and on average sampled the airstream ~ 4 times/min. Three of the 4 turtles showed little change in the time spent in each quarter of the tank during DMS exposure as compared with the control period (Fig. 3). Turtle 2 shifted from swimming mostly upwind during the control period to swimming mostly into the left quarter during the experimental period. For all the turtles, there was no significant shift in the distribution of time between the control and the DMS odor exposure periods (2-tailed Wilcoxon signed-rank $t = 21$, $n = 14$, $p = 0.78$). Just 1 of the 4 turtles spent any time in the upwind quarter of the

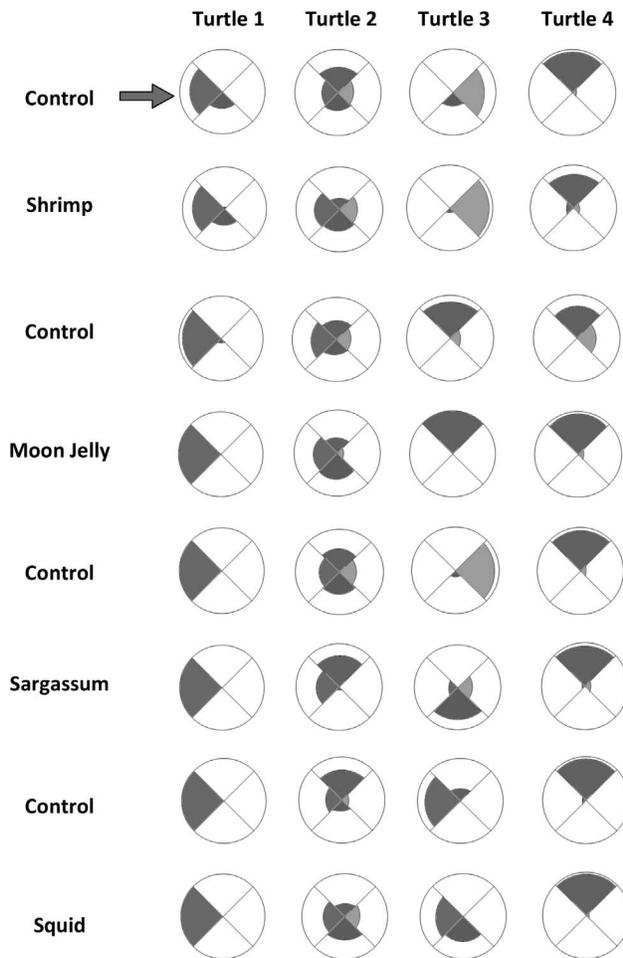


Figure 4. Orientation responses shown by 4 loggerheads during their 5-min seawater control, each of which preceded a 5-min prey odor presentation. To facilitate comparisons, responses are shown in the same order for all of the turtles, but prey odors were presented to each turtle in a different sequence. Note that for most of the turtles in most of the experiments, the introduction of a prey odor does not result in a change in orientation compared to the preceding control period. See the text for the statistical analyses.

tank during the DMS presentation while 2 turtles spent time there during the control period. The result was that the turtles on average spent more time orienting upwind during the control (1.63 min) than during the DMS (1.03 min) tests.

Tethered Turtles: Response to Prey Odors. — Four loggerheads exposed to airborne prey odors (Fig. 4) swam throughout their trial and showed no statistical differences in the distribution of time spent swimming in any tank quarter during the seawater control vs. the prey odor exposure periods (Wilcoxon signed-rank test; $p = 0.42$ – 0.84 for individual turtles). The turtles also showed no significant change in the time spent swimming in the upwind tank quarter during the control odor periods as compared to the prey odor periods (Fisher exact test, 1 df, $p > 0.5$).

Free-Swimming Turtles: Response to Squid Odor. — In these experiments we tested 5, 3-turtle groups of green

Table 1. The number of bites delivered to the tank walls, plastic ball, or to other turtles by 15 loggerhead turtles while swimming freely in groups of 3 in the test tank during consecutive 5-min trials. Groups were size-matched. During each of the 2 control trials, the turtles were exposed to the odor of treated seawater presented in air or as a solution by injection into the water. During the odor trials, the turtles were exposed to squid odor in air (paired with a treated seawater injection under water) or as a solution injected into the water (paired with the airborne odor of treated seawater). Odor descriptions and analyses are in the text.

Bites directed at:	Airborne		Waterborne	
	Control	Squid odor	Control	Squid odor
Tank	0	21	0	44
Ball	3	87	0	77
Turtles	0	4	0	22
Totals	3	112	0	143

turtles and the same number of loggerheads ($n = 15$ turtles of each species). Biting by both species increased significantly during exposure to squid odor compared to the preceding control periods (Tables 1 and 2). Air- and waterborne squid odors evoked a statistically similar increase in biting by loggerheads (112 vs. 143 bites, respectively, compared with an expected average of 125 bites, Table 1; $\chi^2_1 = 1.66$, $p = 0.20$). Waterborne squid odor presentations, however, elicited significantly more bites from green turtles than did airborne odor presentations (298 vs. 172), compared with an expected average (of 235, Table 2; $\chi^2_1 = 16.7$, $p < 0.001$). During both squid odor presentations (in air, in water), both species bit the ball more than the tank walls or the other turtles combined (loggerheads, 164 vs. 91, $\chi^2_1 = 10.1$, $p < 0.01$; green turtles, 285 vs. 185, $\chi^2_1 = 10.3$, $p < 0.01$). The total number of bites observed during exposure to squid odor (airborne and waterborne tests, summed) was significantly greater for green turtles ($n = 470$) than for loggerheads ($n = 255$) as compared with an expected average (of 362; $\chi^2_1 = 32.6$, $p < 0.001$).

Free Swimming Turtles: Response to DMS. — Four, 3-turtle groups of loggerheads ($n = 12$ turtles) were used in these experiments. No turtles displayed any biting behavior during the DMS presentations. One turtle directed 2 bites at the tank wall during a control period.

Table 2. The number of bites delivered to the tank walls, plastic ball, or to other turtles by 15 green turtles while swimming freely in the test tank during consecutive 5-min trials. Turtles were tested in 5 separate groups of 3 size-matched individuals. Format, as in Table 1. See the text for details.

Bites directed at:	Airborne		Waterborne	
	Control	Squid odor	Control	Squid odor
Tank	16	51	2	26
Ball	15	118	3	167
Turtles	6	3	1	105
Totals	37	172	6	298

DISCUSSION

The goal of these experiments was to determine how marine turtles respond to DMS and prey odors that might be detected at a distance from or within productive oceanic hotspots and then use that information to locate prey. We hypothesized that an important component of this response should be some form of orientation. In the absence of detailed observations on how such a search might be conducted for most species under natural conditions (exceptions are discussed below), we could only speculate as to how these behavioral responses might be organized. We hypothesized that if stimuli were detected in air and at a distance from the source, an anemotaxis might occur. However, if the odor was detected under water it might elicit a search in the immediate area for potential targets in the water column.

Responses of Tethered Turtles to Airborne Odors. — We tested the first hypothesis by observing how tethered turtles responded to airborne odors flowing across the water surface. We opted for the use of tethered subjects because this procedure facilitates the measurement of orientation and because in previous studies done with different species of marine turtles, orientation responses were shown to a diversity of stimuli. These include odor-containing water currents, light sources varying in spectral composition, models of prey, change in magnetic field characteristics (inclination angle and intensity), and surface waves (Salmon and Lohmann 1989; Wyneken et al. 1990; Lohmann and Lohmann 1994, 1996; Lohmann et al. 1995; Constantino and Salmon 2003; Gless et al. 2008). In the experiments reported here 12 turtles (4 leatherbacks, 8 loggerheads) failed to change their orientation and swim upwind into any of the odors (Figs. 2–4). Examination of the video records did not reveal other plausible changes in behavior associated with odor exposure such as an increase in the rate of activity or a change in diving frequency or duration. Our data suggest, instead, that airborne odors moving across the water surface are insufficient to elicit an anemotaxis in juvenile leatherback and loggerhead turtles, at least under the simplified laboratory conditions imposed by our experimental design.

However, under field conditions the presence of an odor carried by prevailing winds might indeed result in oriented swimming if those winds produced surface waves. Previous experiments have shown that hatchling marine turtles orient into those waves (Wyneken et al. 1990) and can distinguish between “upwave” and “downwave” directions based upon the sequence of orbital motion that they experience (Lohmann et al. 1995). We hypothesize that odors carried by winds may release a search for the odor source and that this search is then directed (that is, oriented) by the waves those winds generate. An analogous system appears to underlie how captive leatherbacks in shallow tanks orient toward waterborne odors of prey detected in a current. The odors

release a search, which is then directed by the water currents (Constantino and Salmon 2003).

Still another possibility is that the odors we presented were delivered at too high, too low, or too irregular a concentration to evoke an orientation response. That explanation might apply in particular to our DMS trials in which the turtles were initially presented with a highly concentrated and strong odor, but one that rapidly declined in strength because DMS is so volatile and evaporates rapidly. We noted that by the end of a 10-min trial, we were unable to detect any trace of DMS on the filter paper used to introduce that substance into the tank airspace. However, this explanation fails to account for the absence of an orientation response to prey odors, as these persisted throughout the experimental trials.

Responses of Free-Swimming Turtles to Prey Odors and DMS. — In contrast to the tethered turtles, free-swimming turtles showed a clear response to squid odor delivered in air or introduced as an extract delivered in water (Tables 1 and 2). The form of the behavioral response, which was much the same for both loggerheads and green turtles, was typical of other studies done on fishes and aquatic turtles in which a food odor is presented under water and that odor triggers a search (Valentinčič 2004; Bels et al. 2008). In the absence of either a current, a steep concentration gradient, or a visual reference, the movements evoked are characterized by an increase in activity (such as the circling observed by Endres et al. 2009) and the initiation of a random search, as reported in some of the older literature on fishes (Kleerekoper 1967) and turtles (e.g., Mahmoud 1968; Emlen 1969; Burghardt 1970; Manton 1979). In the presence of a current prey, odors elicit a rheotaxis, but in both loggerheads and leatherbacks a visual target is required to orient toward prey (Constantino and Salmon 2003; Southwood et al. 2007). In the field, orientation toward and consumption of jellyfish captured in the photic zone is almost certainly mediated by visual cues (Salmon et al. 2004; Heaslip et al. 2012; Wallace et al. 2015). Our results (Tables 1 and 2) extend those observations to loggerheads and green turtles that preferentially directed most of their bites toward a stationary, suspended visual target (the perforated plastic ball).

Manton et al. (1972) took advantage of these response relationships by training green turtles to associate an underwater olfactory stimulus with a visual target (signal key) that, when contacted, resulted in a food reward. Once trained, the turtles demonstrated that they could detect a variety of compounds (alcohols, aldehydes, esters, and tertiary amines). Rendering the turtles anosmic (by swabbing the nasal cavity with a zinc sulfate solution) temporarily abolished those responses, suggesting that they were mediated by olfaction and not taste. However, because the palate is incomplete in marine turtles, the zinc sulfate solution might also have affected their taste receptors.

Both loggerheads and green turtles performed more bites when presented with waterborne than with airborne squid odor; green turtles did so to a statistically significant degree (Table 2). However, we cannot say whether those differences reflect a stronger reaction to odors detected under water than to those detected in air, as the stimulus concentrations in air and in water were unknown and the quantitative differences in response by both species were confounded with the order of stimulus presentation. The absence of a comparable biting response when turtles were exposed to DMS suggests that this compound plays a different (and presently unknown) role in the search for near-by prey.

Locating Productive Oceanic Hotspots: Some Speculations. — Our data suggest that marine turtles use waterborne food odors to search for prey in the immediate vicinity (Constantino and Salmon 2003; Southwood et al. 2007). However, the failure of airborne odors to elicit an anemotaxis suggests that alternative or additional mechanisms are probably used to locate oceanic hotspots from a distance (Lohmann et al. 2008). Below, we review the literature, emphasizing in particular the nature of these alternative or additional mechanisms.

With few exceptions, the information presently available is largely based upon tracks obtained from instrumented and experienced turtles (e.g., Hays 2008; Benson et al. 2011; Luschi et al. 2013; Dodge et al. 2014). These tracks have enabled investigators to reconstruct the migratory routes of older juvenile and adult turtles and to determine how aspects of their behavior (such as diving frequency, duration and depth, swimming speed, and path straightness) change once they locate what are presumed to be rich foraging locations. These data also show that the turtles, returning either to nesting beaches or to foraging sites, often migrate on remarkably well-oriented paths, ones that suggest they know where they are going. Experiments with juvenile (Lohmann et al. 2004) and adult (Luschi et al. 2007) green turtles indicate that magnetic cues play an important role in navigating toward specific goals.

From a behavioral perspective, an intriguing question centers on how such a capability develops in individuals over their lifetime, based upon the assumption that how adults behave can be understood by determining how capacities expressed initially by earlier ontogenetic stages change with age, experience, or both (Alcock 2009). That approach, however, has until recently not been applied to the study of how marine turtles might locate productive foraging sites. Instead, it was assumed that the orientation mechanisms used by older juvenile and adult turtles to find locations were so different from those used by hatchlings that they could only be understood by studying the behavior of the older turtles (Lohmann et al. 2001, 2008; Luschi 2013). The rationale for this approach was that (loggerhead) hatchlings might associate particular geomagnetic characteristics with broad gyre regions, and are inexperienced, whereas older turtles migrate toward

specific geographic locations (that is, they *navigate*) and gain experience by accomplishing those feats repeatedly. Thus, the strategies and mechanisms employed by hatchlings differed from those of older juveniles and adults. A short time ago, that position appeared justified because naïve hatchlings exposed in the laboratory to magnetic fields characteristic of different gyre locations behaved in much the same way: by orienting in directions that promoted their retention within the gyre. Those responses led to the conclusion that hatchlings could only pair detection of magnetic features with orientation responses appropriate to reach broad gyre locations.

What is now known (as a consequence of further experiments) is that (loggerhead) hatchlings were responding appropriately, given their ecological setting, and that at the same time these hatchlings, like older turtles, can discriminate between magnetic bi-coordinates (the turtle equivalents of latitude and longitude; Putman et al. 2011). Thus, hatchlings possess magnetic maps and the potential to navigate to specific locations, but during their early development they choose under most circumstances to locate gyre regions. Those regions are usually on the inside margin of the current system where eddies are commonly generated and where small turtles may benefit by foraging in locations that are especially productive (across eddy currents; Mansfield et al. 2014). Interestingly, the (presumed) foraging movements of these younger and relatively inexperienced turtles once they locate an eddy appear similar to the responses described for older or more experienced (or both) juvenile turtles (Polovina et al. 2006; Mansfield et al. 2009).

Other observations suggest that orienting toward broad goals is common in marine turtles at various stages in their development. In fact, these “regional” searches are characteristic of how leatherbacks routinely seek their prey (Hays et al. 2006; Hays 2008). Female leatherbacks and (to a lesser extent) loggerheads seek out suitable nesting sites along broad coastal regions and can deposit consecutive nests in areas that may be spatially separated by many kilometers.

Hays et al. (2010) and Scott et al. (2014) hypothesized that the early experiences associated with hatchling transport by currents might play a role in determining which geographic areas were used by older turtles as foraging sites. However, Gaspar et al. (2012) were the first to provide data that actually linked patterns of hatchling displacement from specific nesting beaches to the use of foraging sites exploited by the females that nested at those beaches. Their study was designed to determine why leatherbacks that nested with fidelity at 2 beaches, about 100 km apart on the northeast and northwest coast of New Guinea, foraged as adults in spatially distinct oceanic areas (north and south Pacific ocean basins), thousands of kilometers apart (Benson et al. 2011; S.R. Benson, *pers. comm.*, July 2015).

The answers were revealed by when, seasonally, each population nested (during the winter on 1 beach; during the summer on the other beach) and how the surface

currents adjacent to each beach varied seasonally and over several years. Current variation patterns were used to model where the hatchlings, assumed to behave initially as passive drifters, were most likely to be transported. Turtles from 1 beach were most-often carried by currents into the northern Pacific. These turtles were hypothesized as adults to most-likely frequent productive foraging sites along the continental margins of Asia, the Northern Pacific Transition Zone, and the continental shelf adjacent to Oregon and California. Turtles from the other beach were most-often carried into the southern Pacific. They were hypothesized as adults to exploit productive areas along the east coast of Australia and the Tasman Sea. These predictions were bolstered by the satellite tracks of females that nested on each beach. After nesting was done, these females migrated toward and then exploited those predicted foraging sites.

Gaspar et al. (2012) hypothesized that as juveniles, the turtles displaced into each ocean area "... might record the magnetic positions of randomly discovered foraging areas ...", thus setting the stage for their return as adults to forage at those sites. They termed this idea the "learned migration goal" (LMG) hypothesis and suggested that this explanation accounted for why many leatherbacks not only returned to these foraging areas but did so with great accuracy and precision. Given that loggerhead hatchlings have magnetic maps, it is at least plausible that leatherback hatchlings may also have them and so might indeed "... record the magnetic positions of randomly discovered foraging areas". What now remains is the much harder task of providing definitive evidence to support this idea. Currently, the hypothesis is based upon correlations between where hatchlings are transported and where adults forage but not on a direct demonstration that learning (or some other developmental process) is required to establish that relationship.

One approach to tackling this problem, and one that might be potentially useful in answering questions about the development of any sea turtle behavior, is the deprivation experiment (Immelmann and Beer 1989). These experiments prevent exposure to key hypothesized experiences during appropriate periods of each turtle's development. In this instance, that exclusion deprives the turtles during early development of transport by an oceanic current or prior exposure to a productive oceanic area. Would turtles so treated be capable of navigating toward a foraging site or feeding appropriately once one was found? Such an experiment was actually done some years ago using Pacific loggerheads. Polovina et al. (2006) attached satellite transmitters to 2 groups of juveniles that were then released in the ocean. Their movements and foraging activities were subsequently tracked and compared. One (the deprived) group consisted of 37 turtles, 1–3 yrs of age, hatched from eggs and subsequently reared at the Port of Nagoya Public Aquarium. These turtles were released a short distance offshore from the east coast of Japan and about 7000 km to the west of the highly productive

Kuroshio Extension Bifurcation Region (KEBR). That site is frequently exploited by pelagic stage juvenile loggerheads as well as by a variety of predatory fishes. A second group consisted of 6 wild turtles of about the same size and (presumed) age, caught on longlines and released an average of 4500 km to the east of the KEBR. After release, both groups of turtles swam toward the KEBR. While they travelled in opposite directions, they nevertheless swam at about the same speed toward this productive "hotspot". An analysis of their paths revealed that, while all of the turtles made brief forays in other directions, their progress to the east (deprived turtles) or west (wild turtles) was far more pronounced. Once at the foraging grounds, both groups of turtles concentrated their movements at the edge of eddies where productivity was especially enhanced. Both groups also migrated to higher latitudes when the hotspot shifted in its position northward, a seasonally predictable phenomenon. There were no obvious differences in how efficiently the 2 groups of turtles located the hotspot or in their presumed foraging movements once it was found. Experience did not appear to have any effect on performance (Polovina et al. 2006).

These observations on Pacific loggerheads, though confined to 1 species and 1 study, suggest that prior experience of being transported by oceanic currents or exposed to oceanic "hotspots" is not required for young turtles to locate at least some productive oceanic regions later during ontogeny. Instead, the turtles appear to "know" when and where to search for generally productive areas and how to forage efficiently once they find those sites. These results are no more remarkable than those revealed by experiments showing that loggerhead hatchlings, even before they have entered the sea, have magnetic maps that describe the essential features (to a loggerhead turtle) of an entire oceanic gyre. Could those maps also indicate where the turtles are most likely to encounter productive foraging areas? Perhaps they might. For juvenile North Pacific loggerheads, 2 such locations are known: the KEBR and waters offshore of the west coast of Baha, California (Seminoff et al. 2014). In the northern Atlantic, juvenile loggerheads are attracted to the eastern side of the ocean basin and the shallows surrounding the Azores, Madiera, and Canary islands (Carr 1987; Bolten 2003). These seamount areas are especially productive in both the Atlantic (McCarthy et al. 2010) and Pacific (Uchida et al. 1986) ocean basins. But even if the location of these hotspots is actually built into marine turtle magnetic maps (there is presently scant evidence that they are), it is also possible that the turtles might in addition learn where other foraging areas, encountered opportunistically, are located. There is no reason to assume that the ability of marine turtles to locate productive sites must be based upon either learned or innate processes (as proposed by Gaspar et al. 2012 and by Scott et al. 2014). Indeed, such a dichotomous perspective assumes the two are mutually exclusive developmental alternatives whereas studies in other animals reveal they

more often co-occur in complex relationships (such as innate predispositions to learn certain things during sensitive periods of development; Alcock 2009). In marine turtles, imprinting to a natal region is an important example of this process (Lohmann et al. 2013).

Conclusions

Our observations suggest that for marine turtles swimming in open water, prey odors trigger a visual search in the water column. In previous studies done with leatherbacks, prey odors embedded in a current triggered a rheotaxis (Constantino and Salmon 2003). What remains to be determined is whether prey odors in the open ocean can trigger responses to other kinds of directing stimuli, such as the orbital motion of water in waves. These would be especially interesting experiments to do because our understanding of the behavioral mechanisms involved in searching for and finding prey in the open ocean is incomplete (Lohmann et al. 2008).

At a distance from productive sites, avian marine predators, such as the procellariiform seabirds, have the advantage of keen vision (Martin 1998; Nevitt 2008). That capability provides a flying animal with an elevated and panoramic view of surface waters and a potential variety of cues: color discontinuities between water masses that identify convergence zones, the presence of weed lines, slicks, and other flotsam, and the feeding activity of aerial predators at a distance (Nevitt 2000, 2008). The visual acuity of marine turtles in air, however, is poor (Bartol and Musick 2003), making it unlikely that those cues could be discerned, especially from a view confined to a few centimeters above an irregular water surface surrounded by waves. What remains to be determined is how marine turtles solve this problem. Perhaps turtles compensate by developing magnetic maps so early in their ontogeny. Are these maps also used to identify distant areas as likely sites of high productivity? We hypothesize that they might be, but to find out will require some additional experiments, yet to be performed.

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